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PHYLOGEOGRAPHY OF THE AMERICAN WOODCOCK (*SCOLOPAX MINOR*): ARE MANAGEMENT UNITS BASED ON BAND RECOVERY DATA REFLECTED IN GENETICALLY BASED MANAGEMENT UNITS?

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ABSTRACT.—Information on population connectivity throughout the annual cycle has become more crucial, because populations of many migratory birds are in decline. One such species is the American Woodcock (*Scolopax minor*), which inhabits early-successional forests in eastern North America. Although band recoveries have proved useful for dividing populations of this game bird species into an Eastern Region and Central Region for management purposes, these data do not provide enough detail to determine the breeding population of origin of birds recovered on stopover and wintering areas. To obtain more fine-scale data, we undertook a phylogeographic study of American Woodcock populations throughout their primary breeding range in the eastern United States and Canada using mitochondrial DNA (mtDNA) sequences from the hypervariable control region I (CRI) and ND6 gene. Despite high haplotype diversity, nucleotide diversity was low and there was no phylogeographic structure among American Woodcock populations across the species range, with birds from many states and provinces in both management regions sharing identical haplotypes. Results suggest recent or ongoing gene flow among populations, with asymmetric movement of birds between migration flyways. As has been demonstrated for several other avian species in North America, American Woodcock appear to have undergone a rapid population expansion following the late Pleistocene glacial retreat. Thus, a combination of historical demographic factors and recent or ongoing gene flow mask any population structure based on mtDNA that might accrue from philopatry to breeding areas observed in studies of marked birds. Received 27 May 2004, accepted 30 March 2005.

Key words: American Woodcock, gene flow, migration flyways, mitochondrial DNA, mtDNA, phylogeography, population expansion, *Scolopax minor*.

Phylogéographie de *Scolopax minor*: Est-ce que les Unités de Gestion Basées sur les Données de Retour de Bagues Représentent les Unités de Gestion Basées sur la Génétique?

RÉSUMÉ.—Les informations sur la connectivité des populations au cours de leur cycle annuel sont devenues essentielles puisque les populations de nombreuses espèces d'oiseaux migrateurs sont en déclin. Une de ces espèces est *Scolopax minor*, qui occupent des forêts de début de succession dans l'est de l'Amérique du Nord. Dans un but de gestion, les retours de bague se sont avérés utiles pour diviser les différentes populations de cette espèce selon une région est et une région centrale. Néanmoins, ces données ne fournissent pas assez de détail pour déterminer les populations reproductrices qui sont à l'origine de ces oiseaux retrouvées sur

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les aires de halte et d'hivernage. Afin d'obtenir des données à une échelle plus fine, nous avons entrepris une étude phylogéographique sur des populations de *Scolopax minor*, et ce à la grandeur des aires principales de reproduction dans l'est des États-Unis et du Canada en utilisant des séquences d'ADN mitochondrial (ADNmt) de la région de contrôle I hyper variable (RCI) et du gène ND6. Malgré une diversité d'halotypes élevée, la diversité de nucléotides était faible et il n'y avait pas de structure phylogéographique parmi les populations de *Scolopax minor* au sein de l'aire de distribution de l'espèce, étant donné l'existence d'individus qui proviennent de plusieurs états et provinces, appartiennent aux deux régions de gestion et partagent des halotypes identiques. Les résultats suggèrent la présence d'un flux génique récent ou continu parmi les populations, avec des mouvements asymétriques d'individus entre les voies migratoires. Comme ce fut démontré pour plusieurs autres espèces aviennes en Amérique du Nord, *Scolopax minor* semble avoir subi une rapide expansion de population faisant suite au retrait glaciaire de la fin du Pléistocène. Par conséquent, une combinaison de facteurs démographiques d'origine historique et le flux génique récent ou continu masquent toute la structure de population issue de l'ADNmt. Ceci pourrait découler de la philopatrie sur les aires de reproduction, tout comme cela fut observé dans d'autres études avec des oiseaux marqués.

RECENT POPULATION DECLINES of many avian species breeding in North America have highlighted the need for studies of migrating birds throughout the annual cycle (Webster et al. 2002). Information on connectivity between breeding populations and those using various migration stopover and wintering areas is crucial for developing cohesive plans to conserve and manage declining species. Banding data have proved more useful for tracking game birds throughout the annual cycle than for other avian species, because substantial effort has been expended on marking large numbers of individuals and band recoveries from hunters are relatively numerous. Band recoveries are limited, however, even for some species of game birds. Other methods, such as genetic markers and stable isotopes, can now be used to track populations (Clegg et al. 2003).

The usefulness of genetic markers depends on sufficient genetic differentiation structuring populations across their geographic range—differentiation that can accrue only if migratory individuals display strong philopatry to their nesting areas, with limited gene flow among breeding populations. Such genetic geographic structure has been observed for some avian taxa (Wenink and Baker 1996, Zink 1996, Kimura et al. 2002), but not for others even when gene flow is limited (Ball and Avise 1992, Baker et al. 1994, Wenink et al. 1994, Benedict et al. 2003, Van Den Bussche et al. 2003). Mila et al. (2000) suggest that phylogeographic structure is less likely in

species breeding at temperate latitudes, where habitat contractions restricted populations during Pleistocene glacial cycles (Hewitt 2000), than in Neotropical birds.

The American Woodcock (*Scolopax minor*; hereafter "woodcock") is an upland shorebird found in early-successional forests and fields rather than wetlands or coastal marine environments. Its populations have been in decline since 1968 (Sauer and Bortner 1991, Bruggink and Kendall 1995, Kelley 2003). Habitat loss from urbanization, forest succession, drainage and land-use conversion (Owen et al. 1977, Dwyer et al. 1983, Straw et al. 1994), pesticides (Stickel et al. 1965, Wright 1965), environmental contaminants (Scanlon et al. 1979, Scheuhammer et al. 1999), and hunting (Straw et al. 1994) have been suggested as factors that may be contributing to this decline.

Woodcock are distributed throughout eastern North America, with the primary part of their breeding range extending from Minnesota east to New Jersey in the United States and north to Ontario, east to Nova Scotia in Canada (Sheldon 1967). In addition, some woodcock also breed as far south as Texas, east to South Carolina (Roberts 1993), with records in every state within their range (Keppie and Whiting 1994). Woodcock from the primary breeding range migrate to wintering areas in Maryland and Virginia in the north, across the South Atlantic and Gulf states to Missouri and eastern Oklahoma and Texas. However, little is known about where breeding

birds from each locality spend the winter because of the difficulty in following a significant number of birds between breeding and wintering grounds (Wood et al. 1985).

Judging from band recovery data, woodcock use two distinct migration routes between breeding and wintering areas, with relatively little (1–5%) trans-flyway migration (Coon et al. 1977, Krohn and Clark 1977, Owen et al. 1977). These migration routes correspond to the boundaries of the Mississippi and Atlantic flyways on either side of the Appalachian Mountains (Fig. 1). Woodcock in each flyway are managed as separate continental populations known as the Eastern Region and the Central Region (Gregg 1984). However, band recoveries provide only a minimum estimate of distributions even for such a well-studied game species.

Evidence of predictable migration pathways and philopatry of males (Dwyer et al. 1988) and of females (Dwyer et al. 1982, 1988) to breeding areas led to our prediction that woodcock

populations on either side of the Appalachians would show geographic genetic structure, as would regional populations within flyways. We used mitochondrial DNA (mtDNA) sequences of the ND6 gene and the 5' hypervariable domain I of the control region (CRI) to study the phylogeographic pattern of population structure across their range in North America, posing the question: Are current management regions based on band recovery data reflected in genetically based Management Units (MUs, *sensu* Moritz 1994; Fraser and Bernatchez 2001)? Our goal was to use these data to supplement information on migration patterns as a basis for studying population connectivity between wintering and migration stopover areas and breeding areas, for better-informed management of the species.

METHODS

Sample collection.—We obtained samples from states and provinces throughout the primary



FIG. 1. Geographic range map of American Woodcock in North America showing provinces and states within the Central and Eastern regions.

woodcock breeding range from wings sent to the U.S. Fish and Wildlife Service (USFWS) and Canadian Wildlife Service by hunters. We sampled individuals from each of the following regional populations: 6 individuals each from Wisconsin (WI), Michigan (MI), Illinois (IL), and Ohio (OH) and 12 from Minnesota (MN) in the Central Region; and 6 each from Ontario (ON), Quebec (QU), New Brunswick (NB), Nova Scotia (NS), Maine (ME), Vermont (VT), New Hampshire (NH), Massachusetts (MA), Rhode Island (RI), Connecticut (CT), New York (NY), New Jersey (NJ), and Pennsylvania (PA) in the Eastern Region, for a total of 114 birds. We used tissues from woodcock shot during the first week of the hunting season to increase the chance of sampling birds that were breeding in the states or provinces where they were collected, rather than those passing through as migrants.

DNA sequencing.—DNA was extracted from wing muscle tissue using standard phenol:chloroform extractions (Sambrook et al. 1989). Two regions of the mtDNA genome were sequenced: the ND6 gene and CRI. Primers tRNA^{pro}-L (5'-CTCTAAACTATTCTCTGAC-3') and tRNA^{glu}-H (5'-ATTGGTTGGTTCCCGAAGTT-3') were designed from published sequences of woodcock (Mindell et al. 1998) and other shorebirds (Wenink et al. 1994) to amplify the ND6 gene. Primers d-loopL (5'-GACCGGACACAAATTTTCGGT-3') 54 base pairs (bp) downstream from the 5' end of the control region and 437H2 (5'-GGGTTGCTGATTTCACTTGA-3', modified from Wenink et al. 1994), were designed to amplify CRI.

Polymerase chain reactions (PCR; 25 μ L) contained 0.2 mM dNTPs, 10 \times buffer (pH 8.0), 1.5 mM MgCl₂, 0.2 μ M of each primer, 1.25 U Taq polymerase (Perkin-Elmer), and 10 ng DNA template. Amplifications were done in an MJ PTC-100 programmable thermal cycler (MJ Research, Waltham, Massachusetts) using the program: 94°C for 5 min, followed by 34 cycles of 94°C for 45 s, 50°C for 1 min (55°C for ND6), 72°C for 1 min, and a final extension at 72° for 5 min. The resulting amplification products were reamplified to increase the concentration and purified in 30K microconcentration tubes (Nanosep, Stockholm, Sweden). Direct sequencing was done on an ABI 373 stretch automatic sequencer (Applied Biosystems, Foster City,

California). Reverse strands were sequenced to clarify ambiguous sequences.

Phylogenetic analysis.—Sequences were edited and aligned using the Clustal algorithm in SEQUENCENAVIGATOR (Applied Biosystems), as well as by eye. The model of evolution that best fit the data was selected using MODELTEST, version 3.06 (Posada and Crandall 1998). Once the appropriate model was selected, phylogenetic relationships were estimated using maximum likelihood (ML) (PAUP*, version 4.0b10; Swofford 2002). Ruddy Turnstone (*Arenaria interpres*; GenBank accession no. AY074885), Common Snipe (*Gallinago gallinago*), and Eurasian Woodcock (*Scolopax rusticola*) were used as outgroup taxa. Levels of resolution on nodes were estimated by 100 random bootstrap replications of the data. Sequence data have been deposited in GenBank (accession nos. AY864083–AY864193).

Genealogical relationships among CRI and ND6 haplotypes were also estimated using TCS, version 1.18 (Clement et al. 2000), which uses the method of Templeton et al. (1992). This network method allows for the nonbifurcating genealogical relationships often found in population-level studies and estimates the most parsimonious number of mutational changes among haplotypes. It also calculates the frequency of haplotypes in the data set and estimates the probable haplotype outgroup, which correlates with haplotype age (Castelloe and Templeton 1994).

Population structure.—Population genetic structure was inferred by analysis of molecular variance (AMOVA; Excoffier et al. 1992) provided within ARLEQUIN, version 2.0 (Schneider et al. 2000). This analysis was based on mtDNA (female) lineages grouped by region (Central and Eastern) and populations within regions. The null distributions to test significance of the variance components and the pairwise *F*-statistic (F_{ST}) equivalents (ϕ_{ST}) were constructed from 10,000 permutations of the data.

Gene flow among populations, expressed as estimated number of female migrants per generation ($N_{ef}m_f$, where N_{ef} is the genetic effective population size of females and m_f is the female migration rate), was estimated from $\phi_{ST} = 1/(1 + 2N_{ef}m_f)$ (Slatkin 1991). Maximum-likelihood estimates of migration rates between regions were also calculated, using MIGRATE, version 1.7.6 (Beerli and Felsenstein 1999). This method uses

a coalescent theory approach to estimate past asymmetric migration rates ($4N_e m_p$) between populations, taking into account the history of mutations, uncertainty of the genealogy, and different subpopulation sizes (Beerli and Felsenstein 2001). Neigel (2002) suggests that this method is more appropriate than F_{ST} for estimating gene flow between large effective population sizes; however, it has recently been criticized for inaccuracy (Abdo et al. 2004). Beerli counters that their criticism is flawed and suggests a strategy for achieving reasonable estimates of gene flow (P. Beerli pers. comm.). We used 10 short Markov chains of length 50,000, followed by 3 long Markov chains of length 500,000, sampling every 100 trees in each case. For both short and long chains, 10,000 trees were discarded as initial "burn-in." Initial estimates of theta (θ) and gene flow were based on F_{ST} . MIGRATE was run several times, and estimates from five runs were averaged after results stabilized. Although absolute numbers of migrants between populations estimated with these methods may not be accurate, they are likely to be useful for general comparisons (Whitlock and McCauley 1999, Neigel 2002).

Mismatch distributions (distribution of pairwise substitution differences between pairs of haplotypes in a population) were analyzed using the demographic expansion model of Rogers and Harpending (1992) as implemented in ARLEQUIN. Recent population expansions or bottlenecks will generate a unimodal distribution, whereas long-term stable populations or slowly declining populations will have a multimodal mismatch distribution (Rogers 1995). The mismatch distribution is described by $\theta_0 = 2N_0\mu$; $\theta_1 = 2N_1\mu$; and $\tau = 2\mu t$, where the initial effective population size, N_0 , suddenly changes to N_1 at τ units of mutational time, calculated in terms of μ , the mutation rate per generation of the entire nucleotide sequence studied and t , the number of generations since expansion.

RESULTS

Phylogeography.—We amplified 330 bp from the 5' hypervariable CRI, all of the ND6 gene (521 bp) and 36 bp of tRNA^{glu}, for a total of 887 bp. Phylogenetic relationships were estimated using ML with the general time reversible (GTR) model of substitution with random addition of taxa, empirical base frequencies, $ti/tv = 26:1$

(including outgroup), proportion of invariant sites (I) = 0.5585, and variable rates among sites with a gamma (Γ) distribution, $\alpha = 1.75$. One clade of woodcock was resolved with a high level of variability within the clade, but very shallow divergence among haplotypes (0.1–1.1%) that is not structured geographically (ML tree not shown). Although the level of genetic variation in woodcock is high (haplotype diversity [h] for CRI, ND6, and tRNA^{glu} combined = 0.9977 ± 0.0015), the degree of differentiation among haplotypes is low (nucleotide diversity [π] = 0.0036 ± 0.0021).

Parsimony networks based on CRI and ND6 gene sequences illustrate the pattern of shared haplotypes among populations in the Central and Eastern regions and the shallow, reticulate relationships of mutations among them (Fig. 2A, B). There were 17 unique haplotypes for the CRI portion of the sequences, with another 12 haplotypes shared among individuals from various states and provinces in both the Central and Eastern regions (Fig. 2A and Table 1). A similar pattern of variability (22 unique and 10 shared haplotypes) was observed among ND6 sequences, a surprisingly high level of variation for a coding gene—shared haplotypes for ND6 are different in content but similar in nature to those for CRI (Fig. 2B and Table 1). When all sequences are combined, there are 58 different haplotypes among 114 birds, with extensive homoplasy (network not shown).

Population structure and gene flow.—Using combined CRI, ND6, and tRNA^{glu} sequences, hierarchical AMOVA of woodcock populations in the Central and Eastern regions revealed that none of the variation was attributable to differences between migration flyways (–0.04%), essentially none (0.82%) to variation among populations within regions, and the majority (99.22%) to variation among individuals (Table 2). These results support the lack of geographic structure indicated in the phylogenetic analyses and suggest infinite levels of gene flow (based on F_{ST}) among populations and regions of the North American range. Asymmetric maximum-likelihood estimates of gene flow between flyways indicated that gene flow was primarily from the Eastern Region to the Central Region (~3,100 females per generation) but was lower by orders of magnitude from the Central Region to the Eastern Region (only ~5 females per generation).

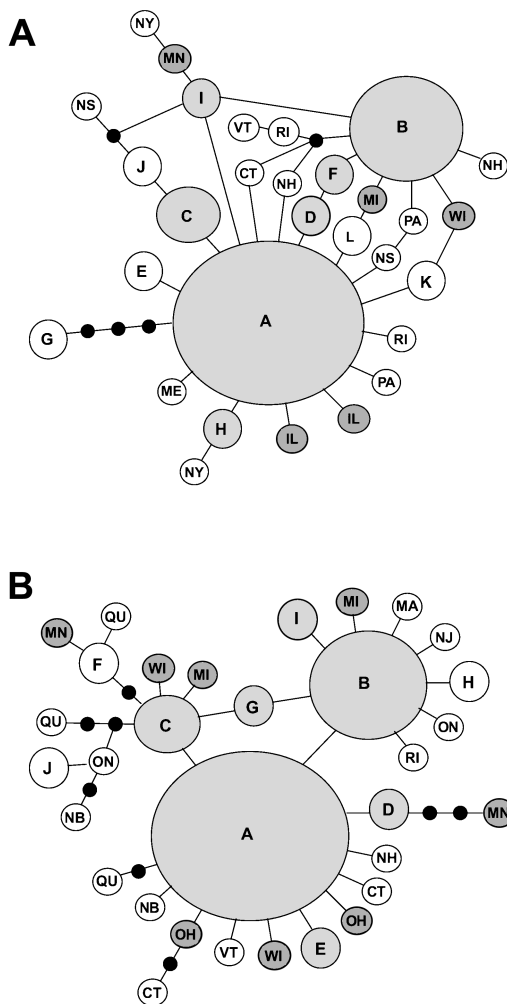


FIG. 2. Estimated networks of most parsimonious relationships among American Woodcock mtDNA haplotypes: (A) control region I (CRI) sequences and (B) ND6 sequences using TCS, version 1.18 (Clement et al. 2000). Solid lines connect haplotypes with a single mutational difference, and small solid circles represent historical haplotypes or current haplotypes not sampled. Dark shaded circles are those haplotypes found only in populations in the Central Region, and open circles are those found only in populations in the Eastern Region. Haplotypes common to both regions are lightly shaded. Haplotype size is proportional to the number of individuals that share the same mtDNA sequence. Letter designations are the same as in Table 1.

A test of goodness-of-fit between observed and expected mismatch distributions revealed that the pattern of mutations among woodcock haplotypes was described by a unimodal distribution for combined ND6 and CRI data ($P < 0.05$) (Fig. 3), suggestive of a sudden, relatively recent population expansion. Parameter estimates were $\theta_0 = 0.0$, $\theta_1 = 2009$, $\tau = 2.808$, which suggests that the population expansion was a 2,000 \times increase in female effective population size N_{ef} . Tajima's (1989) neutrality test rejected the hypothesis of the neutral equilibrium model or population stasis for both ND6 ($D = -2.407$, $P < 0.01$) and CRI ($D = -2.016$, $P < 0.01$) sequences.

DISCUSSION

Phylogeography and historical population structure.—Neither coding (ND6 gene) nor noncoding (hypervariable CRI) sequences, nor total evidence, showed any evidence of phylogeographic structure among woodcock populations throughout their primary breeding range in North America. There are high levels of genetic variability among individuals, as evidenced by high haplotype diversity; however, there is no correlation with geographic region. Haplotypes are shared among individuals from a wide range of populations in both the Central and Eastern regions. An analysis of molecular variance showed that virtually all the genetic variance was distributed among individuals (>99%), with none of it attributable to differences between regions or among populations.

The absence of geographic genetic structure across the range of woodcock may be attributable to recent or ongoing gene flow among widely separated populations or to historical demographic events such as a range expansion from a bottlenecked population (Zink 1997, Mila et al. 2000). Despite a high level of haplotype diversity, haplotypes are primarily separated by only one or two mutations (i.e. nucleotide diversity is low; Fig. 2A, B). A mismatch distribution of woodcock haplotype sequences shows the characteristic unimodal distribution indicative of a sudden population expansion, which suggests that the woodcock population in North America has undergone a recent post-glacial expansion and colonization into the current breeding range. Failure to pass Tajima's (1989) neutrality test also suggests deviations from the

TABLE 1. Management region, sampling location, and number of individuals (n) of American Woodcock sharing haplotypes, based on mtDNA control region I (CRI) and ND6 sequences. Haplotypes correspond to letters in Figure 2.

Haplotype	Migration management region	CRI		ND6	
		Sampling location	n	Sampling location	n
A	Eastern	Connecticut	2		
		Maine	2	Maine	1
		Massachusetts	4	Massachusetts	2
		New Hampshire	2	New Hampshire	1
		New Jersey	4	New Jersey	1
		New York	3	New York	2
		New Brunswick	2		
		Ontario	4	Ontario	2
		Pennsylvania	1		
		Quebec	3		
	Central	Rhode Island	2		
		Illinois	2		
		Michigan	5	Michigan	3
		Minnesota	5	Minnesota	1
B	Eastern	Ohio	4	Ohio	2
		Wisconsin	2		
		Connecticut	1	Connecticut	1
		Maine	2	Maine	2
		Massachusetts	2	Massachusetts	2
		New Brunswick	1		
		New Hampshire	2	New Hampshire	1
		New Jersey	2	New Jersey	2
		New York	1	New York	1
		Ontario	1	Ontario	1
	Central	Pennsylvania	2	Pennsylvania	2
		Rhode Island	1		
		Vermont	3	Vermont	2
		Ohio	2	Ohio	1
C	Eastern	Minnesota	1		
		Wisconsin	1	Wisconsin	1
		Connecticut		Connecticut	1
		Maine	1	Maine	1
		Massachusetts		Massachusetts	1
		New Brunswick	1	New Brunswick	1
	Central	New Hampshire		New Hampshire	1
		New Jersey		New Jersey	1
		New York		New York	1
		Pennsylvania	1	Pennsylvania	1
D	Eastern	Rhode Island		Rhode Island	
		Illinois	1		
		Minnesota	2	Minnesota	1
		Wisconsin	1	Wisconsin	1
		Connecticut	1		
				Maine	1
				New Brunswick	1

TABLE 1. Continued.

Haplotype	Migration management region	CRI		ND6	
		Sampling location	<i>n</i>	Sampling location	<i>n</i>
D	Eastern	Quebec	1	Pennsylvania	1
	Central	Illinois		Illinois	1
		Minnesota	1	Minnesota	1
				Wisconsin	1
E	Eastern			New Brunswick	1
				New Jersey	1
		Ontario	1		
		Rhode Island	2		
	Central			Illinois	1
				Michigan	1
				Minnesota	1
				Ohio	1
F	Eastern	Connecticut	1		
				Ontario	1
				Rhode Island	2
G	Central	Wisconsin	1		
	Eastern			Rhode Island	1
		Vermont	2		
H	Central			Minnesota	1
	Eastern	Nova Scotia	1		
				Vermont	2
I	Central	Illinois	1		
	Eastern	Quebec	1	Quebec	1
J	Central	Minnesota	1	Minnesota	1
	Eastern	Nova Scotia	2	Nova Scotia	2
K	Eastern	Nova Scotia	1		
		Quebec	1		
L	Eastern	New Brunswick	1		

TABLE 2. Analysis of molecular variance (AMOVA) based on combined mtDNA control region I (CRI) and ND6 sequences.

Source of variation	df	Sum of squares	Variance components	ϕ -statistics	Percentage of variation	<i>P</i>
Between regions	1	1.674	-0.0006	ϕ_{CT} -0.0004	-0.04	<0.46
Among populations	16	27.047	0.013	ϕ_{SC} 0.0082	0.82	<0.32
Among individuals	95	152.757	1.608	ϕ_{ST} 0.0078	99.22	<0.30

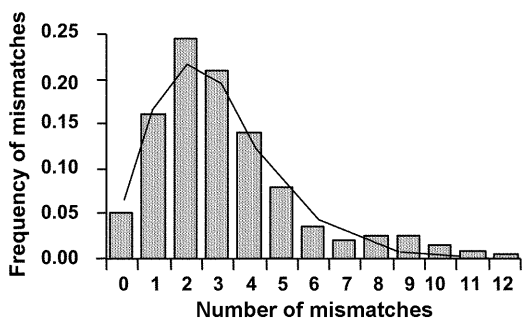


FIG. 3. Pairwise nucleotide mismatch distribution for American Woodcock based on ND6 and CRI haplotypes combined. Solid line indicates expected distribution under the "sudden population range expansion" model of Rogers (1995).

assumption of demographic equilibrium, as has been observed after demographic expansions or bottlenecks in other avian taxa (Fry and Zink 1998, Gay et al. 2004, Rhymer et al. 2004).

Woodcock were likely restricted to southern refugia during periods of glaciation in the Pleistocene, then expanded rapidly north to their current range as the glaciers retreated. The earliest fossil records of woodcock are from the mid-Pleistocene in Florida (Sheldon 1967). Other woodcock Pleistocene fossils have been found in Florida and Virginia; however, the woodcock range between the advance and retreat of ice sheets during the Pleistocene is unknown (Sheldon 1967). Time of divergence among woodcock haplotypes is difficult to estimate—the best calibrated estimates of evolutionary rate for the hypervariable CRI are for Adélie Penguin (*Pygoscelis adeliae*) (Lambert et al. 2002). Even using the minimum mutation rate (0.4 substitutions per site per million years) for our CRI haplotypes, the timing of divergence in woodcock appears to be correlated with a population expansion during the late-Pleistocene glacial retreat.

Gene flow and management units.—In addition to post-glacial population expansion, recent or ongoing female gene flow would further obscure geographic structure despite apparent philopatry to breeding areas (Dwyer et al. 1982, 1988). In an attempt to identify harvest units for management of woodcock, Coon et al. (1977) used the distribution of a relatively small number of band recoveries to identify the configuration of states and provinces for which the

fewest crossovers between migration flyways were observed. Although it is not the configuration with the fewest crossovers, USFWS uses the configuration that conforms to the Atlantic and Mississippi migration flyways to manage woodcock as two separate continental populations. However, in all configurations analyzed, at least 2–4% of bands were recovered in the migration flyway opposite to the one in which birds were banded. One possible mechanism for gene flow is mixing of birds on the wintering grounds, such that some woodcock hatched in one flyway breed in another. For the currently used configuration, banding studies showed that 5% of birds from the Atlantic Flyway were recovered in the Mississippi Flyway and 1% of birds from the Mississippi Flyway were recovered in the Atlantic Flyway (Coon et al. 1977)—a trend similar to that seen in the indirect estimates of movements generated from our genetic data. When analyzed at the scale of regions, maximum-likelihood estimates indicate that most of the gene flow is from the Eastern Region to the Central Region, with relatively little occurring in the opposite direction. This indicates that, in addition to historical demographic factors, some trans-flyway migration is probably ongoing, given that band recoveries are a minimum estimate of direct movements.

Judging from mtDNA sequence data, no distinct MUs (*sensu* Moritz 1994) are evident in woodcock, and genetic criteria cannot be used to separate populations into MUs for decision-making. If current gene flow among populations is limited, more rapidly evolving genetic markers, such as microsatellites, might reveal population structure where phylogeographic analysis of mtDNA did not.

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LITERATURE CITED

- ABDO, Z., K. A. CRANDALL, AND P. JOYCE. 2004. Evaluating the performance of likelihood methods for detecting population structure and migration. *Molecular Ecology* 13: 837–851.
- BAKER, A. J., T. PIERSMA, AND L. ROSENMEIER. 1994. Unraveling the intraspecific phylogeography of knots *Calidris canutus*: A progress report of the search for genetic markers. *Journal of Ornithology* 135:599–608.
- BALL, R. M., JR., AND J. C. AVISE. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. *Auk* 109:626–636.
- BEERLI, P., AND J. FELSENSTEIN. 1999. Maximum-likelihood estimation of migration rates and effective population numbers of two populations using a coalescent approach. *Genetics* 152:763–773.
- BEERLI, P., AND J. FELSENSTEIN. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences USA* 98:4563–4568.
- BENEDICT, N. G., S. J. OYLER-MCCANCE, S. E. TAYLOR, C. E. BRAUN, AND T. W. QUINN. 2003. Evaluation of the eastern (*Centrocercus urophasianus urophasianus*) and western (*Centrocercus urophasianus phaios*) subspecies of sage-grouse using mitochondrial control-region sequence data. *Conservation Genetics* 4:301–310.
- BRUGGINK, J. G., AND W. L. KENDALL. 1995. American Woodcock harvest and breeding population status, 1995. U.S. Fish and Wildlife Service, Laurel, Maryland.
- CASTELLOE, J., AND A. R. TEMPLETON. 1994. Root probabilities for intraspecific gene trees under neutral coalescent theory. *Molecular Phylogenetics and Evolution* 3:102–113.
- CLEGG, S. M., J. F. KELLY, M. KIMURA, AND T. B. SMITH. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's Warbler (*Wilsonia pusilla*). *Molecular Ecology* 12: 819–830.
- CLEMENT, M., D. POSADA, AND K. A. CRANDALL. 2000. TCS: A computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657–1659.
- COON, R. A., T. J. DWYER, AND J. W. ARTMANN. 1977. Identification of harvest units for the American Woodcock. Pages 147–153 in *Proceedings of the Sixth Woodcock Symposium* (D. M. Keppie and R. B. Owen, Jr., Eds.).
- DWYER, T. J., E. L. DERLETH, AND D. G. MCAULEY. 1982. Woodcock brood ecology in Maine. Pages 63–70 in *Proceedings of the Seventh Woodcock Symposium* (T. J. Dwyer and G. L. Storm, Technical Coordinators). U.S. Fish and Wildlife Service, Wildlife Research Report, no. 14.
- DWYER, T. J., D. G. MCAULEY, AND E. L. DERLETH. 1983. Woodcock singing-ground counts and habitat changes in the northeastern United States. *Journal of Wildlife Management* 47: 772–779.
- DWYER, T. J., G. F. SEPIK, E. L. DERLETH, AND D. G. MCAULEY. 1988. Demographic characteristics of a Maine woodcock population and effects of habitat management. U.S. Fish and Wildlife Service, Fish and Wildlife Research Report, no. 4.
- EXCOFFIER, L., P. E. SMOUSE, AND J. M. QUATTRO. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction data. *Genetics* 131:479–491.
- FRASER, D. J., AND L. BERNATCHEZ. 2001. Adaptive evolutionary conservation: Towards a unified concept for defining conservation units. *Molecular Ecology* 10:2741–2752.
- FRY, A. J., AND R. M. ZINK. 1998. Geographic analysis of nucleotide diversity and Song Sparrow (Aves: Emberizidae) population history. *Molecular Ecology* 7:1303–1313.
- GAY, L., D. DU RAU, J.-Y. MONDAIN-MONVAL, AND P.-A. CROCHET. 2004. Phylogeography of a game species: The Red-crested Pochard (*Netta rufina*) and consequences for its management. *Molecular Ecology* 13:1035–1045.
- GREGG, L. 1984. Population ecology of woodcock in Wisconsin. Technical Bulletin, no. 144. Wisconsin Department of Natural Resources, Madison.

- HEWITT, G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405:907–913.
- KELLEY, J. R., JR. 2003. American Woodcock population status, 2003. U.S. Fish and Wildlife Service, Laurel, Maryland.
- KEPPIE, D. M., AND R. M. WHITING, JR. 1994. American Woodcock (*Scolopax minor*). In *The Birds of North America*, no. 100 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- KIMURA, M., S. M. CLEGG, I. J. LOVETTE, K. R. HOLDER, D. J. GIRMAN, B. MILÁ, P. WADE, AND T. B. SMITH. 2002. Phylogeographical approaches to assessing demographic connectivity between breeding and overwintering regions in a Nearctic–Neotropical warbler (*Wilsonia pusilla*). *Molecular Ecology* 11:1605–1616.
- KROHN, W. B., AND E. R. CLARK. 1977. Band-recovery distribution of eastern Maine woodcock. *Wildlife Society Bulletin* 5:118–122.
- LAMBERT, D. M., P. A. RITCHIE, C. D. MILLAR, B. HOLLAND, A. J. DRUMMOND, AND C. BARONI. 2002. Rates of evolution in ancient DNA from Adélie Penguins. *Science* 295:2270–2273.
- MILÁ, B., D. J. GIRMAN, M. KIMURA, AND T. B. SMITH. 2000. Genetic evidence for the effect of a postglacial population expansion on the phylogeography of a North American songbird. *Proceedings of the Royal Society of London, Series B* 267:1033–1040.
- MINDELL, D. P., M. D. SORENSON, AND D. E. DIMICHEFF. 1998. Multiple independent origins of mitochondrial gene order in birds. *Proceedings of the National Academy of Sciences USA* 95:10693–10697.
- MORITZ, C. 1994. Defining “evolutionary significant units” for conservation. *Trends in Ecology and Evolution* 9:373–375.
- NEIGEL, J. E. 2002. Is F_{ST} obsolete? *Conservation Genetics* 3:167–173.
- OWEN, R. B., JR., J. M. ANDERSON, J. W. ARTMANN, E. R. CLARK, T. G. DILWORTH, L. E. GREGG, F. W. MARTIN, J. D. NEWSOM, AND S. R. PURSGLOVE. 1977. American Woodcock. (*Philohela minor* = *Scolopax minor* of Edwards 1974). Pages 149–186 in *Management of Migratory Shore and Upland Game Birds in North America* (G. C. Sanderson, Ed.). International Association of Fish and Wildlife Agencies, Washington, D.C.
- POSADA, D., AND K. A. CRANDALL. 1998. MODELTEST: Testing the model of DNA substitution. *Bioinformatics* 14:817–818.
- RHYMER, J. M., M. J. WILLIAMS, AND R. T. KINGSFORD. 2004. Implications of phylogeography and population genetics for subspecies taxonomy of Grey (Pacific Black) Duck *Anas superciliosa* and its conservation in New Zealand. *Pacific Conservation Biology* 10:57–66.
- ROBERTS, T. H. 1993. The ecology and management of wintering woodcocks. Pages 87–97 in *Proceedings of the Eighth American Woodcock Symposium* (J. R. Longcore and G. F. Sepik, Eds.). U.S. Fish and Wildlife Service Biological Report, no. 16.
- ROGERS, A. R. 1995. Genetic evidence for a Pleistocene population explosion. *Evolution* 49:608–615.
- ROGERS, A. R., AND H. HARPENDING. 1992. Population growth makes waves in the distribution of pairwise genetic differences. *Molecular Biology and Evolution* 9:552–569.
- SAMBROOK, J., E. F. FRITSCH, AND T. MANIATIS. 1989. *Molecular Cloning: A Laboratory Manual*, 2nd ed. Cold Spring Harbor Laboratory Press, Plainview, New York.
- SAUER, J. R., AND J. B. BORTNER. 1991. Population trends from the American Woodcock singing-ground survey, 1970–1988. *Journal of Wildlife Management* 55:300–312.
- SCANLON, P. F., T. G. O'BRIAN, N. L. SCHAUER, AND R. G. ODERWALD. 1979. Lead levels in primary wing feathers of American Woodcocks harvested by hunters throughout the United States range. *Bulletin of Environmental Contamination and Toxicology* 21:683–688.
- SCHEUHAMMER, A. M., C. A. ROGERS, AND D. BOND. 1999. Elevated lead exposure in American Woodcock (*Scolopax minor*) in eastern Canada. *Archives of Environmental Contamination and Toxicology* 36:334–340.
- SCHNEIDER, S., D. ROESSLI, AND L. EXCOFFIER. 2000. ARLEQUIN, version 1.1. A Software for Population Genetic Data Analysis. Genetics and Biometry Laboratory, University of Geneva, Geneva.
- SHELDON, W. G. 1967. *The Book of the American Woodcock*. University of Massachusetts Press, Amherst.
- SLATKIN, M. 1991. Inbreeding coefficients and coalescence times. *Genetical Research* 58:167–75.

- STICKEL, W. H., D. W. HAYNE, AND L. F. STICKEL. 1965. Effects of heptachlor-contaminated earthworms on woodcocks. *Journal of Wildlife Management* 29:132–146.
- STRAW, J. A., JR., D. G. KREMENTZ, M. W. OLINDE, AND G. F. SEPIK. 1994. American Woodcock. Pages 97–114 in *Migratory Shore and Upland Game Bird Management in North America* (T. C. Tacha and C. E. Braun, Eds.). International Association of Fish and Wildlife Agencies, Washington, D.C.
- SWOFFORD, D. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4. Sinauer Associates, Sunderland, Massachusetts.
- TAJIMA, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* 123:585–595.
- TAMURA, K., AND M. NEI. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution* 10:512–526.
- TEMPLETON, A. R., K. A. CRANDALL, AND C. F. SING. 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics* 132:619–633.
- VAN DEN BUSSCHE, R. A., S. R. HOOFFER, D. A. WIEDENFELD, D. H. WOLFE, AND S. K. SHERROD. 2003. Genetic variation within and among fragmented populations of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*). *Molecular Ecology* 12:675–684.
- WEBSTER, M. S., P. P. MARRA, S. M. HAIG, S. BENSCH, AND R. T. HOLMES. 2002. Links between worlds: Unraveling migratory connectivity. *Trends in Ecology and Evolution* 17:76–83.
- WENINK, P. W., AND A. J. BAKER. 1996. Mitochondrial DNA lineages in composite flocks of migratory and wintering Dunlins (*Calidris alpina*). *Auk* 113:744–756.
- WENINK, P. W., A. J. BAKER, AND M. G. J. TILANUS. 1994. Mitochondrial control-region sequences in two shorebird species, the Turnstone and Dunlin, and their utility in population genetic studies. *Molecular Biology and Evolution* 11:22–31.
- WHITLOCK, M. C., AND D. E. MCCAULEY. 1999. Indirect measures of gene flow and migration: $F_{st} \neq 1/(4Nm + 1)$. *Heredity* 82:117–125.
- WOOD, G. W., M. K. CAUSEY, AND R. M. WHITING, JR. 1985. Perspectives on American Woodcock in the southern United States. *Transactions of the North American Wildlife and Natural Resources Conference* 50:573–585.
- WRIGHT, B. S. 1965. Some effects of heptachlor and DDT on New Brunswick woodcocks. *Journal of Wildlife Management* 29:172–185.
- ZINK, R. M. 1996. Comparative phylogeography in North American birds. *Evolution* 50:308–317.
- ZINK, R. M. 1997. Phylogenetic studies of North American birds. Pages 301–324 in *Avian Molecular Evolution and Systematics* (D. P. Mindell, Ed.). Academic Press, San Diego, California.

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